

The distribution, behavioural ecology and breeding strategy of the Pygmy Toad, *Mertensophryne micranotis* (Lov.)

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Introduction

Sexually mature males of the East African pygmy toad, *Mertensophryne micranotis* (Loveridge) have been reported as having series of small spines around the rim of the cloaca and at the entrance to the cloacal tube (Grandison, 1980). Development of these spines correlates with development of the cluster of heavily keratinised thumb spines and their function was interpreted as an adaptation for holding the vents of the male and female securely together during mating to ensure direct transfer of sperm to the small clutch of large eggs produced by the female. Spines in the area of an anuran's vent were first reported by Anderson (1871). He described a large zone of curved cornified papillae in *Rana gammi* Anderson, a species currently synonymised with *Rana (Paa) sikkimensis* Jerdon. Dubois (1976) figured the spines in *sikkimensis* and suggested that cornified spinules occur also in *Rana (Paa) delacouri* Angel. The life histories of neither of these Nepalese species is known.

In order to test the theory that had been postulated of internal fertilisation in *Mertensophryne micranotis* fieldwork and a captive breeding programme were recently undertaken in Kenya. New information on the species' occurrence in Kenya, its habits and breeding behaviour is presented here.

Range and ecological preferences

M. micranotis is known to occur in Tanzania, Zanzibar and Kenya. Few examples have been collected, perhaps because such a small-sized toad (sexual maturity is attained at 16 mm in males) is difficult to detect in leaf litter. Although the type and paratype found at Kilosa, Tanzania and a single individual from the Uluguru Mts. were said by Loveridge (1925) and Barbour & Loveridge (1928) respectively not to have been found in forest, elsewhere the species seems to be restricted to forest or recently cut down forest. In Kenya the species occurs both along the coast from Gede in the north (3°11'S: 40°1'E) to Shimoni in the south (4°38'S: 39°23'E), in the Shimba Hills National Park in the Coast Range (4°16'S: 39°22'E) and Mrima Hill (4°29'S: 39°16'E). Until comparatively recently the Coast Province of Kenya was a near continuous forested belt overlying the approximately three kilometre wide Pleistocene coral reef and the Pliocene and Pleistocene sandy soils adjacent to it farther inland. Today little true forest remains in the Coast Province and very few remnants extend to more than 50 acres. Agriculture, notably plantations of sugar, coconut, cashew nut, maize and sisal combined with the rapid growth of Kenya's tourist industry have taken their toll of the coastal forests. Two of the small remaining pockets are contained in the

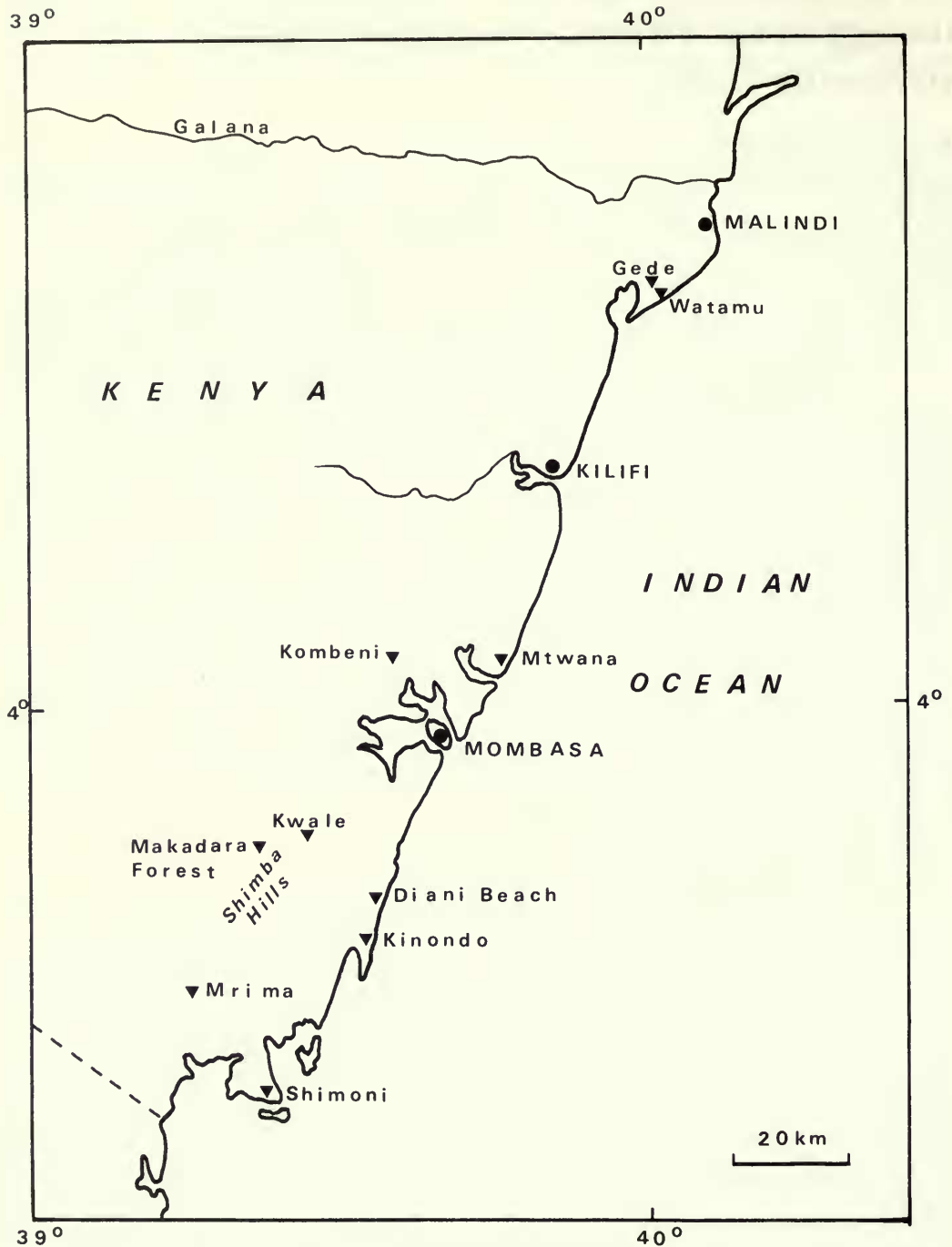


Fig. 1 Known distribution of *Mertensophryne micranotis* (Loveridge) in Kenya. Records indicated by an inverted triangle.

National Monuments of Gede and Mtwana, in which are preserved the ruins of thirteenth century Arab-African towns. Diani forest (sometimes also referred to as Jadini forest) consists of 50 acres of largely untouched forest similar in composition to Gede forest; it is privately owned. Other small forest relics encircle cleared areas that until the nineteenth century were settlements, each housing up to 2000 of the Mijikenda peoples but which today contain only a few houses occupied by elders of the clans and graves of their ancestors. Most of these kayas, as these sacred villages are called, were situated along the ridge of the Coast Range from the Shimba Hills northwards to Kilifi and at vantage points to resist incursions from the north by the Galla farmers. By the seventeenth century the most southerly of the Mijikenda, the Digo, vacated their Shimba kaya and established minor kayas along the coastal plain (Spear, 1978). At one such sub-kaya, Kinondo, and at the Kombeni kaya *M. micranotis* has been found. On account of their religious significance and present day use for rituals and processions the kaya forests are provided with a measure of protection which may safeguard their populations of *micranotis*.

In the southern extremity of the Coast Province two densely forested hills, Jombo and Mrima, jut up spectacularly from the surrounding flat plains (Britton *et al.*, 1980). No herpetological survey has apparently ever been made of Jombo (476 m) but the senior author made two short visits to nearby Mrima which rises to 299 m. The very deeply weathered volcanic plug of Mrima has been prospected since the early 1950s for its rich deposits of manganese and niobium. Its rocks weather extremely rapidly and up to 236 m of terra rosa cover the carbonatite plug. It is the weathered material that has been mined and the abandoned and completely unprotected mineshafts are a serious hazard to contend with when scouring the upper reaches of the forest for the anuran denizens of the leaf litter. A circular, flat-topped pile of moist leaves which contained duiker droppings and may have been a communal duiker latrine on to which some animals, perhaps ants, had piled leaves and other debris yielded juvenile *M. micranotis*. The pile was on a trail and was the only damp spot found; no rain appeared to have fallen for some considerable time and no water-filled treeholes were evident. On the bank of a path and among small pieces of weathered carbonatite and terra rosa and harmonising perfectly in colouration another juvenile *micranotis* was obtained. In these forests there are no surface ponds or streams and even after heavy and prolonged rain the water probably rapidly disappears through the red earth and litter that overly and form pockets in the labyrinth of holes in the coral rag of the narrow coastal strip. On the sandy soils farther inland the rains likewise drain rapidly. The only standing water that becomes available with the highly seasonal rains are ephemeral reservoirs in treeholes formed by broken off limbs, in fissures in tree buttresses and in live and fallen tree trunks, as well as in abandoned shells of the large land snail, *Achatina*, and in the occasional discarded can on the forest floor. Consequently the only anurans that can survive in such forests need to have a highly specialised breeding strategy, such as direct development that completely omits the larval stage or one that produces a terrestrial larva, or need to be opportunistic breeders capable of taking advantage of the seasonal water pockets for egg laying sites. As the water holes are small and subject to rapid desiccation small clutches capable of an accelerated rate of development would be to the species' advantage.

The searches made of the forest litter, of trees and shrubs in these Kenyan forests have revealed only three species of Anura, two of them arthroleptines a group known to develop directly from eggs laid in underground chambers to fully transformed miniatures of the adult frogs. The third, *Mertensophryne micranotis*, has been reported as breeding in water-filled treeholes and land snail shells and has an unusual-shaped tadpole with an angled head that is surrounded by a raised ring of tissue (Grandison, 1980). The anuran composition of a waterless forest in SE Tanzania is recorded by Loveridge (1942). The area is Nchingida 10°8' S, 39°12' E on the Rondo Plateau which is the type locality of *Mertensophryne micranotis rondoensis* (Loveridge), a form that Loveridge distinguished from the nominate on its less heavily pigmented throat. Loveridge (1944) described the Rondo Plateau as waterless where even the heaviest rainstorms drain rapidly through the sandy soils. In addition to the *M. m.*

rondoensis he recorded (1942, 1944) four other species of Anura—two arthroleptines and two microhylids, *Breviceps mossambicus* Peters and *Spelaeophryne methneri* Ahl. While the life history of *Breviceps* is known to be entirely independent of water (Wager, 1965), very large eggs being laid in burrows often far from water and the tadpole stage passed within the egg capsule, no aspect of the breeding cycle of *Spelaeophryne* has been recorded. The right ovary removed from an adult female *S. methneri* in the BM collections contains 18 large ova, average diameter 2 mm, and a few much smaller ova: all are unpigmented. Such a small clutch of unpigmented eggs suggests a specialised reproductive mode that has freed the species from an aquatic environment, although since the species lacks any obvious means of burrowing into the litter, unlike *Arthroleptis stenodactylus* Pfeffer and *Breviceps* with their well developed shovel-shaped metatarsal tubercles, it seems unlikely that *Spelaeophryne* is a burrowing breeder. Perhaps like *Nectophrynoides malcolmi* Grandison (1978) it has a terrestrial tadpole with a vascularised tail that serves as a respiratory organ, but perhaps like *Mertensophryne micranotis* it depends on waterfilled holes in which to lay its small complement of eggs.

The senior author's field study was conducted during the month of May. Mean monthly rainfall records had suggested that this period would be the most likely to coincide with the long rains and consequently produce water-filled breeding sites and the likelihood of witnessing breeding behaviour in the species. However the rains were capricious in May 1981 and at Diani Beach in the southern coastal belt only 19 cm fell during the entire month and for half the period there was no rain or only a few drops (C. Harcourt, pers. comm.); as a result the number of water-filled treeholes and land snail shells was exceedingly small and no mating pairs were found. The standing water in all treeholes found was siphoned and checked for the presence of anuran eggs and tadpoles but only one sample contained *micranotis* tadpoles; it was in one of three holes in the buttress formation of a tree that branched near its base into three trunks and was the only one obscured by a green leafy liana which partly shaded it from the sun. The diameter of the tree trunk at the level of the hole was 54 cm. The other two waterfilled holes in the same tree were at a similar height from the forest floor and although their sizes fall within the range of variation of other oviposition sites for *micranotis* the holes contained only insect larvae (Table 1). All the tadpoles, in excess of 45, had developed limbs but still had larval mouthparts. The pH of the water was not taken and the identity of the tree is not known.

The mammalogist, Dr G. Rathbun, reports (pers. comm.) that while studying elephant shrews and cutting forest trails at Gede he was attracted by a faint squeak to a hole in a tree

Table 1 Records of water-filled treeholes occupied by *Mertensophryne micranotis*. From data supplied by G. Rathbun (†) and L. P. Lounibos (*)

Location	Date	Height from forest floor (cm)	Diameter (cm)	Depth (cm)	Volume of water (cc)	Larvae (L) or Toads (T)
† Gede	18.v.71	150.0		10.16	Full	T (♂ and ♀)
* Kombeni	16.v.75				700	L
	16.v.75				230	L
	24.iv.76				90	L
	24.iv.76	30.48	3.8 × 5.1	5.08	55	L
	27.iv.76	101.60	3.8 × 7.6	7.62	20	L
	7.v.77				60	T (in amplexus)
* Makadara	11.iv.76	17.78	2.5 × 2.5	6.35	70	L
	11.iv.76	96.52	2.5 × 2.5	6.35	25	L
	19.iv.76	121.92	3.8 × 3.8	7.37	45	L
Shimoni	12.v.81	20.32	2.5 × 3.8	10.16	Full	L

7.6 cm diameter which he tentatively identified as *Lecaniodiscus fraxinifolius*. The hole was in a stump formed by a fallen limb 1.5 m from the forest floor. It contained a pair of sexually mature *M. micranotis* which suggests that the hole had been selected as a potential breeding site. Dr L. P. Lounibos (pers. comm.) provides the only other known records of the occurrence of *micranotis* in water-filled treeholes. His records and details of the Gede and Shimoni treeholes are given in Table 1. Dr Lounibos' observations were made in the course of his research into mosquito habitat segregation in Makadara Forest Shimba Hills and Kombeni Forest, Rabai Location (3°55'S: 39°34'E). Samples of his Makadara Forest tadpoles and adults were identified by A. McKay, National Museums, Kenya and the identity of a sexually mature male obtained at Kinondo Forest was confirmed by the senior author. It is assumed that his Kombeni tadpoles and toads were also correctly identified. Lounibos (1981) should be consulted for rainfall records and seasonality of water in treeholes in his study areas.

Movements, colour change and territorial behaviour

Skulking movements and exceptionally effective camouflage are striking features of *M. micranotis*. Adults and subadults when disturbed on the forest floor tend to remain motionless or to very slowly back under a dead leaf or twig or disappear down a hole. A gravid female unearthed from loose soil at the base of a tree flattened its body and remained inert for some time after capture and to the extent that it resembled a dead leaf.

The disruptive dorsal colour pattern of shades of brown closely matches the leaf litter in which *micranotis* is usually found and makes the animal exceedingly difficult to detect. The darkest areas of the body are invariably the lateral band and the interocular bar. A pale hair-like vertebral line of variable length, but usually extending from behind the eyes to the sacrum is present in most specimens. It is sometimes flanked by an irregular dark brown band that divides in the sacral region to form a large ring enclosing a pale zone which extends posteriorly to a brilliant white supra-anal triangle. This white triangle is characteristic of the species. The dark vertebral band and ring are separated from the even darker lateral band by a broad lighter area which is particularly subject to variation in colour according to the animal's background. For instance, in an adult male transported on white plastic foam this dorsolateral area was a very pale grey but after a day spent on dead leaves, twigs and bark the entire dorsum changed to dark brown, while two days later the pale grey areas changed to khaki. Both in its dark and khaki phases the toad was barely discernible among the litter. Recently transformed juveniles and halfgrown individuals are usually black when they emerge from their hiding places but may acquire a greenish-brown tinge when more active. Ventrally, both adults and young have prominent dark blotches on a white background. Males tend to have a brighter, more contrasting colour pattern than females. Observations on captive individuals suggest that the species is diurnal and particularly active in the morning, also that it is territorial, with individuals having their own burrows in the leaf litter. In the wild it is likely that members of the species occurring in forest overlying coral rag will use as retreats the abundant holes in the coral as well as burrows in soil and leaf litter. After active foraging the toads usually back down into their burrows. Adults are more secretive than juveniles and were not seen to make their presence obvious by hopping or other rapid movements; their movements were exceedingly slow, laborious and consisted of usually no more than five steps at a time followed by a long pause. On the other hand, juveniles tended to scramble and hop but such activity was interspersed with long periods of immobility.

The junior author noticed the species' propensity while in captivity to climb. Day old toadlets climbed with apparent ease the glass sides of a casserole in which they were reared. Generally they moved hand over hand with the body raised but when climbing clean glass they lowered their bodies. Adults not only readily climbed the plants in the terrarium, occasionally roosting on leaves and crawling along narrow stems but they persistently climbed the glass sides of the rectangular tank usually by straddling a corner of the terrarium

and bracing their limbs. As they climbed the glass it was noticed that they left behind a trail of liquid and that the posterior part of the toad's abdomen was flattened on the substrate. It is believed that the liquid is expelled from the toad's cloaca and that the surface tension set up facilitates progression over a smooth surface. By developing a technique that allows a short and spindly legged species to climb smooth vertical surfaces the availability and variety of treehole oviposition sites may also be increased thus enhancing the chances of survival.

Captive breeding programme

One subadult and eleven juveniles collected between 29 June and 11 July 1981 were reared in captivity to sexual maturity. They were collected from an area of less than an acre in the vicinity of the junior author's house at Watamu. The area once covered by primary forest and an extension of the Gede Forest was cleared of all but the large trees for house building in 1980. The toads were found on and among the leaf litter overlying coral rag in or at the edge of a surveyor's cut line as well as in a large termite-ridden rotten log in the undergrowth.

The terrarium consisted of a glass tank $40 \times 28 \times 22.5$ cm furnished with a 2–5 cm layer of leaf litter and sand, growing plants and logs. A coconut shell with a little rain water and a plastic jar 12 cm deep and a 6 cm diameter, filled with rainwater and tilted at an angle of 45° against a twisted root provided potential oviposition sites. The root acted as a climbing frame and provided numerous hiding places. A wooden ramp in the jar of water formed an exit.

By the 22 October, five days after the rains had started the day temperature exceeded 30°C and night time temperature 25°C and there was high humidity, the first batch of eggs was laid but neither mating nor egg laying was witnessed. Several toads appeared gravid.

The following accounts are condensed from the detailed notes made by the junior author on her observations on the mating behaviour of her captive specimens.

Courtship

It remains uncertain whether females approach individual males and what signals are used to initiate courtship because pairs were already in amplexus on each occasion when observations were begun. However it was noticed that the soft chirp of a male in amplexus prompted three other males that had been chasing each other around in the water container to call and mount each other indiscriminately and their calls appeared to induce two females to move in the direction of their calls but stop and wander off when the calling ceased. The behaviour of the three males in the jar suggests that the normal calling-station may be a water-filled container and that the receptive female moves in that direction when stimulated by the advertisement call. However the mating behaviour of only six pairs has been observed and while one pair mated in water the other pairs mated mostly out of water. Visual as well as auditory cues may contribute to mate selection in *M. micranotis* for it was noted that the three calling males in the water jar were of a brighter colour and more contrasting pattern than the amplexic male which was very dark coloured.

Amplexus and fertilisation

The mating of one pair, which spanned a period of over eight hours, is described in detail. When the male first mounted the female, their eyes were in the same vertical plane while his hind legs trailed on the ground. The amplexic position was axillary. As he drew up his legs he stimulated the female's sacroiliacal region by drumming it with his long fourth toe then placed his feet over her tibiotarsal joints. Half an hour later he uttered an almost inaudible rapid ticking sound which the female answered with a soft chirp. The pair were clamped closely to each other from snout to vent but although their white supraanal patches were vertically in line a distance of about 2 mm separated them. After an interval of about a few

minutes the female alternately inflated and deflated her body, as if sighing, while his feet were placed on her flanks. As her body deflated at 30 second intervals the male exerted a downward squeeze with his cloacal region. Despite the female moving away and trying to dislodge the male by scratching him first with her hind leg then with a front leg, the male remained firmly attached, although at one point he was shifted sideways as she forced her way under a piece of bark. Mating movements were discontinued while the female fed on white ants but were resumed approximately two hours after observations on the amplexic pair were begun. The male resumed tactile stimulation of the female by drumming his fourth toe. His heels which were then placed on either side of and slightly above her white supraanal patch seemed to channel the drop of clear liquid that trickled from his cloaca down to hers where it appeared to be absorbed. As the female adopted a more upright stance the male moved farther back and lower down and his mating movements became more forceful. As he engaged in a series of thrusts his white supraanal patch was seen to curl inwards towards that of the female. During the ensuing two hours mating movements continued intermittently, with a rest period while the female, still with male attached, moved to a hiding place in the litter but when the amplexic male produced a rapid, very faint ticking sound another male called from 25 cm away in the water jar; the vocalisation elicited a marked increase in activity by all the other males in the terrarium which chased and mounted each other indiscriminately while their calls became louder until each call sounded like a ten note chirp which could be heard 2.5 m away. Several females were active on the floor of the terrarium but although one of the calling males attempted to mount a female it did not persist when the female moved away. When the amplexic pair emerged from the hiding place more vigorous mating movements occurred, despite the female's attempts on two occasions to dislodge the male, and he thrust twice each time the female deflated her body. Although both sexes were visibly vibrating no call from the female was audible but the male emitted a ticking sound. During the next hour sporadic mating movements occurred but his vent was above hers and although the pair entered the coconut shell partly filled with water and moved round the slope in a clockwise direction only her foot entered the water and the pair climbed out of the shell. The female again tried to dislodge the male while she ate insects. Observation was discontinued for ten minutes during which time the pair disappeared.

In five other pairs in which mating was witnessed the duration of amplexus varied from five and a half hours to ten hours. It was noticed that the male's grip on the female's vent is so tight that his vent drags upwards the skin surrounding her vent. One pair found in the water jar in the 'normal' amplexic position were joined by a second male which clung to the female's axillae in an inverted, belly to belly position. Both males engaged in mating movements but two hours later when the dorsal male had disappeared the protruding cloacal region of the underslung male was seen to curl upwards to contact that of the female and the moisture he expelled from his vent as he thrust appeared to immediately be absorbed by the female. Belly to belly amplexus is known to occur also in the internally fertilised Ethiopian bufonid, *Nectophrynoides malcolmi* Grandison (Grandison, 1978 and Wake, 1980).

Although clutches of eggs were later found in the jar of water in the terrarium, egg laying by mated females had not been witnessed and because males were present the possibility of the eggs having been externally fertilised could not be ruled out. So on the next occasion when a pair began to mate they were removed to another terrarium containing a water bowl of similar capacity and quantity of water. When mating was completed and the male had dismounted he was removed and returned to his original terrarium. Mating had taken place in water. Six hours after mating the female, still in the water, began laying eggs, two strings emerging together. Three and a half hours from the start of egg laying and at 2300 hours oviposition had not been completed, but the following morning two egg strings containing a total of 22 eggs were found attached to the rim of the jar. The female had returned to the floor of the terrarium. The eggs proved to be fertile and they developed at a similar rate to those in previous clutches. Each of the six eggs in one string that was severed and preserved within forty minutes of being laid was found to be at the late cleavage stage of development, but eggs

from another clutch where the time of laying was unknown were at early to late gastrula. The number of eggs in five clutches were 17, 19, 22, 32, 32.

The foregoing description emphasises the close contact of the cloacae during mating in *Mertensophryne micranotis* and the tenacious grip that the male exerts on the female's vent while he engages in downward thrusts and his feet are placed on each side of the female's vent. While it can be assumed that the male's cloacal spines play a significant part in the coupling and that internal fertilisation of the eggs takes place it is still not known whether the spines interlock in the furrows of the female's vent.

Function of the tadpole's head 'crown'

Broadley (in Channing, 1978) suggested that the function of the head 'crown' in tadpoles of *Stephopaedes anotis* (Boulenger) might be to exclude from the eyes and nostrils scum accumulating on the water surface. The angled head and ring of raised tissue ('crown') of the *M. micranotis* tadpole is closely similar to that of *S. anotis* (Grandison, 1980) but observations on tadpoles of *M. micranotis* in the wild and in captivity suggest that the angled head with the raised ring of tissue surrounding a saucer-like depression in which lie the eyes and nostrils is a simple adaptation for suspending the tadpole at the meniscus, where the highest concentration of oxygenated water is available in the small pocket of stagnant water that is selected as a breeding site. With the 'crown' breaking the water surface the tadpole has access to oxygen, both during its gill breathing stages and later when it has acquired lungs, at the same time maintaining itself in a tail-down position with the minimum expenditure of energy. In the field study it was noticed that each time the sun struck the water surface of the treehole the tadpoles tended to rise quickly and suspend themselves at the meniscus, particularly around the rim of the hole so that their angled heads were parallel to the contour of the meniscus whilst the body and tail of the tadpole hung down vertically. In such a position the ventral mouthparts had access to the algal growth lining the rim of the cavity. When the head 'crown', which is at an angle of 45° to the body and tail, breaks the surface tension at or near the centre of the hole where the meniscus is virtually horizontal the body and tail of the tadpole are suspended parallel to the angle of the head.

Diet

The contents of the stomachs of three subadults that were known to have been preserved immediately after capture were analysed. Ants constituted the major food element but mites were found to have been almost equally favoured, particularly *Linopodes* (Eupodidae). Although nine other genera of mites were present only one or two examples of each were identified (*Eupelops*, *Trachygalumna*, *Pilizetes*, *Liodes*, *Eremaezetes*, *Scapheremaeus*, *Bdella* and *Spinibdella*). Beetles and thrips of kinds typical of the litter/subcortical layer were also represented in the analysis, as well as Collembola (*Symphyleona*) and the macerated remains of spiders and fly larvae. The only trace of termites was a crumpled set of wings of Termitidae. In captivity the toads thrived on a diet of small white ants, termites and aphids.

Acknowledgements

This study was supported by the Fauna and Flora Preservation Society and the British Museum (Natural History). Field work was made possible through the assistance of the Office of the President of Kenya and the cooperation of Mr A. D. McKay, National Museums of Kenya. The senior author thanks Drs L. P. Lounibos and G. Rathbun for making available their observations on treehole occupancy by *M. micranotis*; her colleagues Dr W. Sands and Miss A. Baker for analyses of stomach contents; Miss C. Harcourt for field

assistance and rainfall records; and Mr and Mrs M. McKay and Mrs D. Webb for kind hospitality. The assistance given by Dr R. C. Drewes, Mr S. Reilly and Mr E. Wederkinch in making material and field data available is also gratefully acknowledged, as is Professor Ruth Bellairs' cooperation.

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